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The unit of shoot growth in dicotyledons. By ANNIE M. GRIFFITHS, B.Sc., and MARJORIE E. MALINS, B.Sc. (Communicated by Professor PRIESTLEY.)

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I—*Introduction*

Recent work on the growth of the Angiosperm shoot has raised again the fundamental question of the way in which a shoot is constructed. Two possibilities present themselves, either the various phases of growth may follow one another in regular succession as one passes back from the apical meristem, or differentiation may occur discontinuously in a series of steps. The latter conception suggests the possibility of discontinuous development of the vascular system also and such isolated parts might serve as osmotic centres, which would have considerable bearing on the question of food supply to the apical meristem. If the development is discontinuous, the shoot may be regarded as being built up of a series of segments or units of growth, which are obviously very closely integrated, so that they will only be detected upon a close analysis of the process of shoot development.

The usual conception of the shoot is that it is an axis, differentiated into node and internode, the node being the level of insertion of one or more leaves, and similarly, in any conception of the shoot as a segmented structure, it seems obvious that the leaves must be an important factor.

If, then, any evidence is to be forthcoming for the segmentation of the shoot, it will most probably be found in plants with a simple type of phyllotaxis with only one leaf inserted at a node and the orthostichies as few as possible. The development of plants with alternate, spiral, and decussate phyllotaxis has therefore been examined from this point of view.

II—*Historical*

The various theories of shoot construction which have been put forward from time to time fall into three main categories—

(*a*) Theories regarding the stem as the fundamental structure of the shoot and the leaves as mere appendages of it.

(*b*) Theories regarding the leaves as the basal structures, which either largely or entirely build up the shoot.

(*c*) Theories which regard the shoot as built up of a number of segments or phytons, which comprise leaf and stem and sometimes the root as well.

The classical literature is discussed in some detail by Chauveaud[2] and only those theories which have direct bearing on the present work are briefly mentioned below. Čelakovský[1], on purely theoretical

grounds, regarded the leaf, node, and internode as differentiated from a common shoot zone and together forming an entity. He distinguished between two types of shoot segments (sprossglieder), the holocyclic, where the segment comprises the whole cross section, and the mericyclic, where it comprises the sector of the stem included between the two radii bounding that fraction of the circumference which is occupied by the theoretical leaf initial. The segments, according to him, are semicircles in cross section in plants with alternate or decussate phyllotaxis and smaller fractions in types with more complex phyllotaxis.

Chauveaud[2] put forward a phyton theory, in which the unit consisted of a leaf and an associated root (phyllorhize). He worked out its application in sporelings of *Ceratopteris thalictroides*, but applied it also to Angiosperms. In Dicotyledons, he regarded the absence of roots in connection with the upper leaves as being compensated by the development of additional vascular strands from the leaf into the common axis, composed of fused units. Hofmeister[8] (*loc. cit.*, p. 520) enunciated and Nägeli[9] supported a conception of the shoot axis as a stem clothed by a covering of leaf tissue. On the same lines and based on external morphological features, Saunders[13] has put forward her "Leaf-skin Theory of the Stem."

As a result of the study of the physiological conditions governing shoot growth, the unit of growth in an alternate-leaved plant (*Vicia Faba*) has been defined as "the segment of the axis, which subtends a leaf initial and surrounds its vascular strand as it differentiates . . . . which runs downwards from a leaf insertion to the foliar gap above the insertion of the next leaf vertically below."[12] This definition gives the same unit for alternate-leaved plants as Čelekovský's theory, but differs in the conception of the unit for decussate plants (Fig. 8).

III—*Morphology and anatomy of the adult shoot*

(*a*) Phyllotaxis alternate

Pisum sativum

The plant has a somewhat irregularly 4-angled stem, the stipulate leaves being inserted alternately at the opposite, more acute angles. The leaf, at its insertion, enwraps more than half the stem—the stipules lying over the lateral corners—so that the outline of the shoot axis in section varies considerably according to the level at which it is cut.

In section below a node, the stem shows the leaf trace bundle of the leaf above in the most strongly marked angle and also a bundle in each lateral corner. The remaining six to eight bundles lie in a ring nearer the centre of the stem. When the leaf trace enters the stem, it is joined by a lateral bundle on either side. These latter bundles link the leaf trace with the lateral corner bundles by an arch,

from which the stipule bundles are given off. The leaf trace then runs down uninterrupted through two internodes, gradually passing nearer to the central ring meanwhile. It then forks, the two branches pectinating with the outgoing leaf trace at the node, and running down through a further internode before joining into the central ring. The lateral corner bundles pass down vertically through one internode and then pass into the central ring, the corner angle in the next internode being supplied with a bundle in connection with the alternate leaf on the other side of the stem.

De Bary[4], using Nägeli's figures, describes a very similar course for the bundles in *Lathyrus*. A full account of seedling anatomy for *Vicia Faba* has been given by Goldschmidt[7] and for the Leguminosæ by Compton[3]; a general account of node and internode anatomy for *Vicia* and *Pisum* has also been supplied by Priestley[11].

(*b*) Phyllotaxis decussate

Syringa vulgaris and Ligustrum vulgare

The stem is oval in section, the long axis of the oval alternating through a right angle in successive internodes. The leaves are borne in opposite and alternating pairs, and since each leaf insertion occupies more than a quarter of the circumference of the stem, there is only a narrow groove running down the side of the stem between the insertion of the two leaves of a pair (Fig. 4).

In section, the stem shows a complete ring of vascular tissue very early, but the course of the leaf traces can still be distinguished by the presence of large vessels which are not developed in parts of the vascular ring not in direct continuity with leaf traces. Each leaf trace bundle runs down undivided through two internodes; it then forks and pectinates with the outgoing leaf trace. The two branches can be followed down through two further internodes and then die out. Consequently twelve traces can usually be distinguished in the vascular ring in the adult internode.

Mentha sp., Coleus sp.

The stem is square in section and the leaves are inserted in opposite and alternating pairs at the sides. The leaf vascular supply enters the stem as two bundles, which separate and pass immediately to the corners of the stem, where they run down undivided through two internodes and then die out. Similar bundles enter at the next node, so that in section of the stem, the leaf trace xylem is represented by a pair of bundles at each corner. When the ring of vascular tissue is completed, which it is relatively early in *Mentha*, the leaf traces can still be distinguished by the presence of vessels. A small lateral bundle is usually present in the middle of each side of the vascular ring; this arises as a branch from one or both leaf traces as they enter the stem and pass to the corner positions. The bundle runs down through two internodes, forks and dies out.

IV—*Development*

The growing point of the shoot appears as a central dome on which arise lateral folds—the leaf initials. The outer layers of cells are entirely meristematic, the first signs of vacuolation appearing behind the centre of the dome in the future pith cells. The future cortex is the next tissue to vacuolate—the intervening ring of meristem cells elongating and becoming the procambial ring. The vacuolating cells elongate in the direction of the long axis of the shoot and at the same time divide repeatedly—almost entirely by transverse walls—so giving rise to "strings of cells," the original outlines of which are evident for a considerable time, especially in alternate-leaved plants. This latter phase of growth is the "Rippen meristem" stage described by Schüepp[14] (*loc. cit.*, p. 18). These cells eventually cease to divide and undergo final extension, when the grouping into "strings" is no longer recognisable to any appreciable extent. These three stages of cell differentiation have been described in detail by Priestley.[12]

The stage of final cell extension seems to be initiated nearer to the growing point in decussate and spiral types than in the alternate, and also seems to be delayed by growth in the dark.

In the procambial ring, the first elements to differentiate are those of the protophloem. These cells are recognised in cross section by their thick, refractive walls, which stain deeply with light green. The protophloem elements also lose their contents earlier than any of the surrounding procambial cells.

In *Pisum*, protophloem differentiation was recognised in connection with the youngest leaf rudiment, but in the decussate types not until the third or fourth pair of leaves. In every case, where protophloem was observed, it could be traced back and found to be in direct continuity with the phloem of the older parts of the plant, evidently developing continuously from older into younger tissues. In *Pisum*, where the stem bundles remain relatively distinct for a considerable time, the phloem follows a course similar to that described for the bundles, passing as a single strand down through two internodes, then forking and passing down through two further internodes before losing its identity.

In the decussate type, where a vascular ring is developed early, the phloem strands do not retain their individuality, but form a cylindrical network of anastomosing strands.

The first protoxylem elements are differentiated in the procambial ring at a slightly greater distance from the shoot apex than the first protophloem. In *Pisum*, no xylem was recognisable in the youngest leaf rudiment, which already showed protophloem, and in those rudiments which showed xylem and phloem—such as the second in *Pisum* and the third or fourth in the decussate types, the phloem was always found differentiated beyond the xylem. Protoxylem differentiation, in all the types examined, was initiated in isolated cells lying at the junction of leaf and stem. At the stage at which

xylem first becomes recognisable, there has been practically no elongation of the internode and the procambial cell which differentiates into the first protoxylem element may extend through an entire internode, or even further. The differentiation of the first element is followed by similar changes in the cells in contact with it above and below, so that the first strand consists of a single series of differentiated elements, which is common to leaf and stem, but which is not in continuity with the xylem of older parts of the plants until a much later stage of development. Even when protoxylem strands of different systems do eventually come into close contiguity in the vascular ring, they appear to be separated from one another by a parenchymatous cell, though it is possible that this intervening cell may lignify in still older tissues. This type of xylem development as isolated systems, common to leaf and stem, was verified for *Pisum, Helenium, Mentha, Coleus, Syringa,* and *Ligustrum.*

Similar origin of leaf trace xylem in isolated systems was observed by Flot[6] in *Lonicera caprifolium* and was also described by Nägeli[9] for thirty-four Dicotyledons and two Gymnosperms. Nägeli concludes that it is evidently the general type of development for Dicotyledons, though exceptions may occur, the one cited by him being *Begonia.*

V—*External evidence for shoot segmentation*

1—*Ring marking experiments*

The development of vascular tracts affects the differentiation of the tissues surrounding them. It has been shown that the primary vascular tracts—the leaf trace bundles—run down through two internodes and it is obvious that, in plants where only one leaf is inserted at a node, tissues will occur at the same level of the stem, which are in the sphere of influence of vascular tracts at different stages of development. The results of this method of shoot organisation may be seen by following the course of final cell extension up a growing shoot, and such a method of growth organisation must affect the behaviour of the shoot as a whole.

In the following experiments, equidistant rings were drawn in Indian ink round a young shoot, which was still elongating. The subsequent distribution of cell extension was shown by separation of the rings, which was sometimes accompanied by their distortion.

In *Pisum,* growth caused the rings to become more widely separated. In the youngest internodes that it was found possible to mark, the rings separated at the base of the internode first, but in somewhat older internodes, the base had evidently reached its final extension before marking, and only the upper parts showed separation of the rings. Separation of the rings was accompanied by distortion, the rings becoming more widely separated on the side of the stem below the next leaf insertion and so developing an upward inclination towards the centre of the leaf (Fig. 1).

The distortion of the rings shows that the two sides of the pea stem are reaching the stage of final extension at different times. The separation of the rings indicates that extension passes uniformly up the side of the stem from one leaf to the next on the same side, that being also the tissue in which the leaf trace runs down undivided through two internodes. The tissue to reach final extension first is that just above a leaf insertion, the earlier phases of vacuolating and dividing cell growth continuing longest just below the leaf insertion. This is so marked that extension may be more active just above a leaf than just below it, though the latter point is further removed from the shoot apex. It appears then that final cell extension in

FIG. 1

FIG. 2

FIG. 1—*Pisum sativum*, showing the effect of growth on equidistant, horizontal rings.

FIG. 2—*Vicia Faba*, showing the effect of growth on equidistant, horizontal rings.

the shoot axis is initiated in a number of steps, each step corresponding to a tissue unit, consisting of the growing cells surrounding a leaf trace bundle in its vertical course to the next leaf on the same orthostichy—in this case through two internodes. In *Pisum*, two units of this type always face one another on the opposite sides of the stem in relation to the alternate leaves.

When two units of this kind of different ages are developing side by side, it is obvious that the rings will only remain horizontal at points where the basifugal differentiation in the lower half of the younger unit keeps pace with that in the upper half of the older unit. The particular pattern of ring distortion in *Pisum* indicates that, just below a node, the younger segment reaches the stage of final extension before the top of the older segment just below the leaf (Fig. 1).

In *Vicia Faba* the inclination of the rings is reversed (Fig. 2), suggesting that, in this plant, the top of the older unit is extended before the younger unit at the same level. In *Phaseolus multiflorus* the first two leaves are inserted at the same level, the upper parts of the plant showing normal alternate phyllotaxis. In this case, rings

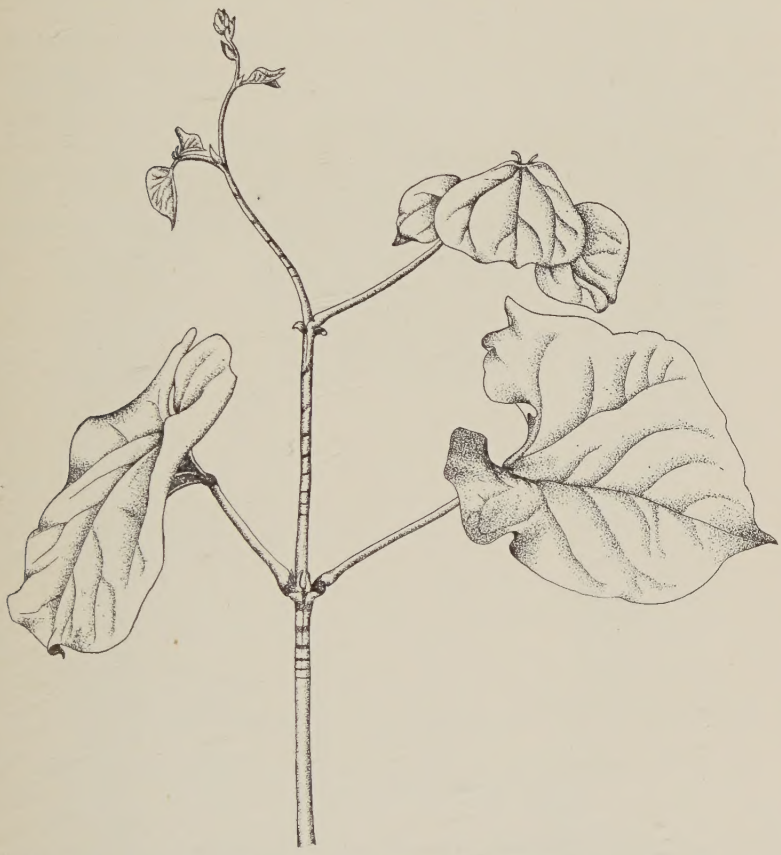

FIG. 3—*Phaseolus multiflorus*, illustrating the effect of growth on equidistant, horizontal rings.

below the basal pair of leaves showed no distortion, although the stem was still elongating in this region as evidenced by separation of the upper rings. In the region of alternate leaves, the same type of distortion was shown as in *Pisum* (Fig. 3). Similar ringing experiments were carried out on plants with spiral phyllotaxis of about 2/5. In all these types, *Nicotiana*, *Solanum tuberosum*, *Cineraria*, and *Helenium*, the margins of the leaves were extended down some little

distance below the leaf insertion as wings on the stem. The disappearance of the wings and the general outline of the stem showed that the adjacent units overlap one another to some extent. In all cases the rings separated more towards the upper end of the unit and became slightly distorted upwards just below a leaf insertion, but owing to the more numerous units at any level, the results were less marked than in the alternate types.

In decussate types, as in the alternate, separation of the rings at the base of the internode only occurred in the youngest examples ringed; in all the others, separation occurred only at the top. The decussate plants on which ring experiments were carried out, fell into two groups. In one group, represented by *Mentha*, *Coleus*, and *Mercurialis*, the rings separated but showed no distortion. Examination of these plants showed that the leaves of a pair extend so far round the stem as to meet (Figs. 4, 8b), and consequently the rings

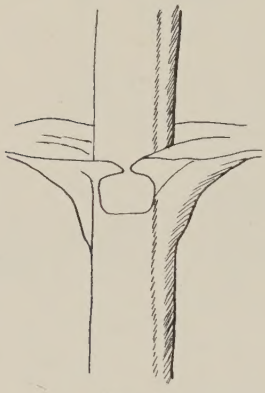

FIG. 4

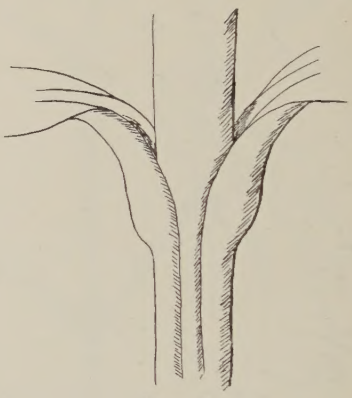

FIG. 5

FIG. 4—*Mentha*, showing the way in which a pair of leaves completely enwrap the stem.

FIG. 5—*Syringa*, showing the insertion of a pair of leaves, which do not completely enwrap the stem.

show no distortion, since the surface tissues are developing in connection with differentiating leaf traces of approximately the same age at any level. In the very youngest leaves, in regions too young to ring, the leaves do not quite meet round the stem, and it appears to be the marginal growth of the leaf, continued over the surface of the stem, that results in the complete overwrapping. In the second group, *Syringa*, *Ligustrum*, *Vinca*, and *Acer*, the stem is grooved on either side, between the pair of leaves inserted at the node above, so that the two leaves do not completely enwrap the stem (Figs. 5, 8c). In these cases, the rings separated as before and also showed slight distortion, the rings dipping down at the grooves. As the vascular

[*Photo. by J. Manby*]

FIG. 6—Specimen of *Mentha*, showing spiral torsion.

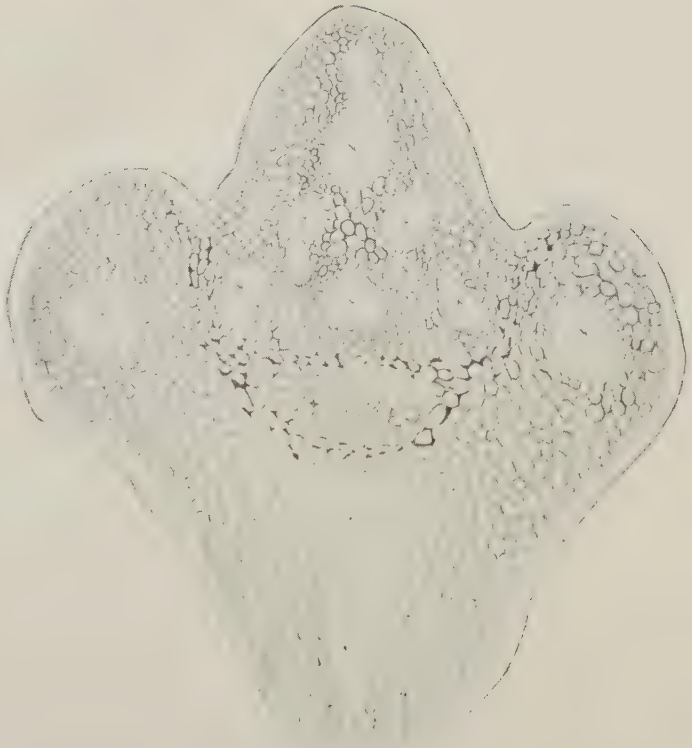

Fig. 10—T.S. Stem of *Pisum*, showing the deeply staining "line of strain" (× 35).

Fig. 11– L.S. *Pisum* through the region of strain caused by the insertion of a leaf (× 80).

tracts in *Ligustrum* and *Syringa* extend down primarily through two internodes, it is probable that the units will also, in which case the grooves represent the only exposed surface of the lower half of the younger units, and the behaviour of the rings conforms with the *Pisum* type. That the units in decussate types do extend through two internodes receives striking support from abnormal specimens of *Mentha* showing spiral torsion[10]. The leaf scars in these specimens are situated one above the other in close proximity and describe a

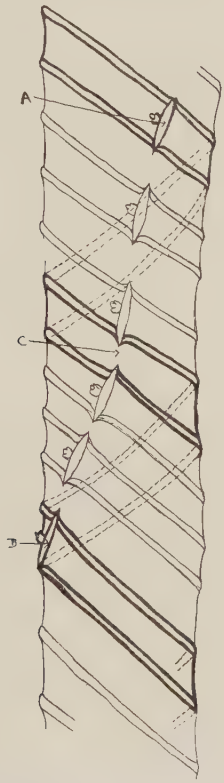

Fig. 7—Diagram, illustrating spiral torsion of *Mentha*.

spiral round the stem. This spiral is in the opposite direction from the ribs which run spirally down the stem from the leaf scars. If one follows a rib from the insertion of one leaf to the next on the same rib, one crosses the spiral line of leaf scars halfway between the two, indicating that the unit from a leaf extends through two internodes (Figs. 6 and 7). Similar cases are recorded by De Vries.[5] The fact that the unit in decussate plants extends through two internodes, and that four units are consequently present at any one level (even

though only two of these units may be represented at the surface of the shoot) is emphasised as it is in disagreement with Čelakovský's figures, where the unit for decussate plants is represented as occupying half the section of the stem and as extending down through one internode only (Fig. 8a). The difference between the two conceptions is shown diagrammatically in Fig. 8.

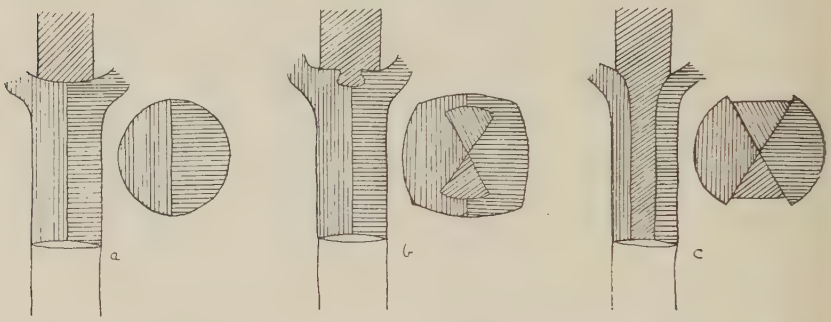

FIG. 8—Diagrams illustrating units of shoot growth in decussate plants.

(*a*) Čelakovský's theoretical unit.
(*b*) Unit in *Mentha*.
(*c*) Unit in *Syringa*.

2—*Plumular hooks*

Further evidence for differentiation of the units at different times is provided by the phenomenon of nutation, and also in the formation of a plumular hook, when certain kinds of plants are grown in the dark.

In longitudinal sections and also by careful maceration of the tissues, the progress of the vacuolating and dividing cell stage may be followed by counting the number of cells in a string which has arisen by the division of a common mother cell. It is found that this stage, like the final extension, proceeds upwards from the base of a unit. A considerable number of cells—up to 16 or more—constitute a string in the lower or middle region of a unit, but just below a leaf insertion the number of cells in the string is fewer, often only two or three, and these strings are also deflected from their longitudinal course out towards the leaf base. The difference in the number of cells in a string at the two sides of the stem may be sufficient to push the apex over to one side, which will be reversed as other units reach the same stage, giving rise to such movements as fall under the heading of nutation.

In plants grown in the dark, the vacuolating and dividing cell stage is unusually prolonged, so that the differences described above are more marked than in plants grown in the light and result in a complete pushing over of the apex into the form of a hook. In one case in *Pisum* it was found that the strings at the convex side of the

hook consisted of 16 cells, whilst those on the concave side consisted of 8 or fewer. As an older unit ceases to grow actively, whilst a younger one at the same level begins to grow more vigorously, it is obvious that the direction of the hook will be slowly reversed (Fig. 9).

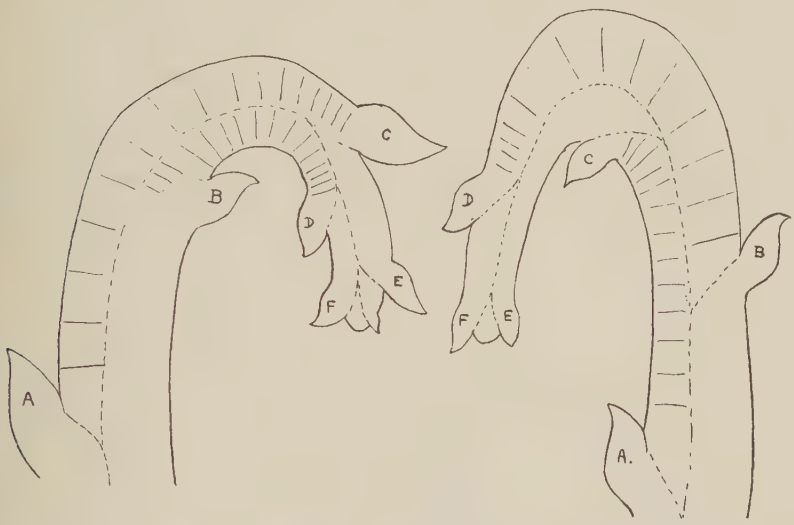

FIG. 9—Diagram showing the reversal of plumular hooks in *Pisum*.

VI—*Internal evidence*

When units at different stages of development are growing in such close juxtaposition as exists in the shoot, it is probable that there may be a region of strain between the two.

In following down serial transverse sections in *Pisum*, a striking effect is noticed along the line of fusion of leaf and stem. The cells in this region appear narrower and stain deeply with light green or methylene blue, their appearance suggesting the idea of a line of strain (Fig. 10). The appearance persists for many sections below the leaf entry, but gradually becomes less marked and finally quite indistinct in the lower half of the internode, where alone the flattened shape of the cells is reminiscent of the condition. As one passes in review sections in series downwards from a node, the "line of strain" moves inwards until finally the orientation of the pith cells indicates that it runs across the middle diameter of the stem.

The line of strain is also recognisable in longitudinal sections (Fig. 11), even when the staining effect is not evident, by the cells being narrower and dividing less regularly than the surrounding cells, which divide entirely by transverse walls. It is suggestive that this

"line of strain" is most evident in that region of the stem which also shows maximum distortion of the rings.

In etiolated plants, where the vacuolating and dividing cell stage is more prolonged, the strain between the two units is more marked than normally and may become so intense that splitting is often the result (Fig. 12). This offers, perhaps, the strongest evidence for the presence of strains.

In decussate plants, there is less evidence of strains and no indication is visible in the pith. There is, however, some evidence just below a leaf entry and also in *Mentha* and *Coleus*, where the older units have joined up over the younger units at the sides. The line of strain is here indicated by the same type of deep-staining tissue and the effects gradually disappear as one passes down the internode.

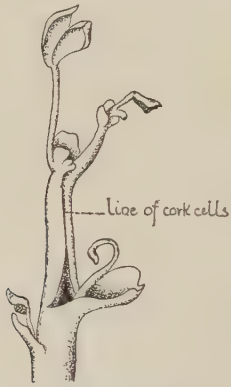

Fig. 12—Etiolated plant of *Pisum*, showing splitting of the tissues.

VII—*Conclusions*

From the cases cited by Nägeli[9] and the additional cases verified in this work, it is clear that it is usual in Dicotyledons for the protoxylem to originate in a series of isolated systems, which arise at the junction of leaf and stem and are common to both from the first, whether the leaf trace is single, as in *Pisum*, *Helenium*, and *Syringa*, or double, as in *Mentha* and *Coleus*. The first initiation of protoxylem is in a single cell of the procambial strand. This cell is at first an elongated cell densely filled with protoplasm and differing from the cells of the apical meristem merely in shape and position. The cell to become xylem first lies in contact with the vacuolating cells of the future pith and the first sign of differentiation is the earlier vacuolation of the future xylem element as compared with the neighbouring procambial cells. Vacuolation proceeds rapidly, and instead of the cell divisions which accompany vacuolation in the

neighbouring pith cells, the protoplasm tends to break down, and in doing so must add organic solutes to the sap in the vacuole. Such a cell may act as an osmotic centre and draw water from any neighbouring tissues. At the stage when this first xylem element is differentiating, there has been practically no elongation of the internode in which it is developing, and the single element may extend through one or more internodes and consequently is not far removed from older xylem systems in connection with the next lower leaf. The solution in these older xylem systems is relatively dilute and the new osmotic centre will withdraw water from them across any intervening cells as across a semi-permeable membrane. The new element, as it continues to differentiate, becomes more permeable and when all its protoplasm has broken down it is completely permeable and its contents are lost to the surrounding cells. It is probably the sap then supplied to them that causes the cells of pith and cortex to vacuolate, extend, and continue to divide, pulling out the original xylem elements as they do so. Meanwhile, procambial cells above and below the first xylem element differentiate in similar manner, so that as the surrounding tissues elongate, the first vascular strand comes to consist of a series of protoxylem elements, joined more or less end to end. Such a process of xylem differentiation proceeds upwards into the leaf and downwards into the stem, where it is interrupted eventually by the vascular system of the next leaf below, so that the uninterrupted course varies with the phyllotaxis, consisting of two internodes in alternate and decussate types and more in spiral types, e.g. five in 2/5 phyllotaxis. The way in which the protoxylem elements first act as osmotic systems as they vacuolate and then become completely permeable, losing their sap to the surrounding tissues, indicates how the developing strands affect the surrounding tissues, and why the shoot differentiates in definite tracts which are closely associated with the course of the leaf trace bundles. When the leaf trace has developed down to within a very short distance of the leaf trace below, it does not make actual contact with it, but forks and the outgoing leaf trace pectinates with the two arms of the fork. The xylem tracts are, however, brought into close proximity and the transfer of sap would appear to be more rapid, as the cells of the younger unit above take in water, and undergo final extension—this phase always working up from the base of a unit, as shown by the ring experiments.

When only two leaf trace bundles are developing at any one level —as in the case of alternate-leaved plants—there is a possibility that the sphere of influence of the individual tracts may be fairly clearly defined. This is illustrated by the marked results obtained in the ring experiments in *Pisum*, the indication of lines of strain and the strong development of the plumular hook.

Where, however, several leaf trace bundles are developing at any one level, as in spiral and decussate plants, it is to be expected that

the spheres of influence of each vascular tract should be less clearly defined, and that the factors affecting the differentiation of one tract should affect also, to some extent, the neighbouring tracts. So one finds in spiral and decussate types that, although the rings show slight distortion, practically no evidence of internal strains between the units can be detected.

The way in which the vascular system develops and the general process of growth proceeds, makes it impossible to regard leaf and stem as separate entities, and the unit of growth suggested agrees closely with that formulated by Čelakovský's theory[1] with the exception of the decussate type, to which reference has already been made. The further downward development of vascular tracts, after forking and pectinating with the outgoing trace, is probably what Chauveaud regards as the development of additional elements into the common axis to compensate for the suppression of roots in relation to the higher "phyllorhizes" in Dicotyledons. The theoretical conception of the exact nature of the segment is, however, of less significance than the important physiological effects resulting from the discontinuous xylem development. The development of such local osmotic systems in the young tissues not only causes the growth and differentiation of the shoot tissues to take place in definite tracts, which are here regarded as the units of shoot growth, but probably are also important in relation to the supply of solutes to the apical meristem.

VIII—*Summary*

The development of the shoot has been followed in plants with alternate (*Pisum*) and decussate phyllotaxis (*Mentha, Coleus, Syringa, Ligustrum*).

The protophloem, as it develops, is always continuous with the phloem further down in the axis. In every case xylem differentiation in the procambial strand proceeds in a series of isolated steps, always starting anew at the base of each leaf initial in the course of its development.

This method of xylem differentiation probably means that the young tissues immediately round each leaf trace are irrigated with sap and solutes in the early stages of its differentiation. Their growth and division are probably determined by this sap supply, hence the tissues of the axis fall into a series of growth units, the extent and distribution of which are determined by the method of leaf insertion.

Units of shoot growth are thus distinguished on grounds of development which closely resemble the "sprossglieder" of Čelakovský[1] in the case of alternate and spiral-leaved plants, but differ in detail in the case of decussate plants.

Equidistant rings, marked on young shoots, are separated and distorted by subsequent growth. The results obtained by such experiments, and also the formation of plumular hooks in etiolated

plants, support the conclusion that units of growth at different stages of development are present at the same level of the axis.

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